The spatial and temporal heterogeneity of macrophyte communities in thirty small, temporary ponds over a period of ten years.

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Abstract.

Ponds are important habitats within many landscapes because of the diversity of wildlife they support. This arises in part because of the heterogeneity of ecological communities found in neighbouring ponds but this variation has proved difficult to explain. Chance and unrecorded historic events have often been emphasised as explanations. This study describes the development of spatial heterogeneity and the role of historic events in the development of pond plant macrophyte communities from the ponds' creation until ten later using thirty small, adjacent temporary ponds in Northumberland. Plant communities showed significant spatial variation from the first year onwards. Metacommunity spatial patterns changed over time but even after ten years several distinct macrophyte communities persisted in different ponds. The outcome was that a greater variety of pond communities persisted than was likely if a single, larger pond had been created on the site. The spatial patterns of the plants communities were compared to spatial variation of summer dry-phase and winter inundation. Macrophyte heterogeneity appeared to result from deterministic change which would have been difficult to detect in a snap-shot survey not knowing the history of the ponds. Winter inundation showed significant spatial trends every year which mirrored the changing distribution of macrophyte communities between ponds. The proximate influence of the inundation is ultimately determined by the position of each pond in the landscape so that the marked spatial and temporal heterogeneity of plant communities was strongly influenced by small scale variation in hydrology The results suggest that the heterogeneity of pondlife across a landscape may be deterministic when recorded over a longer time period and not due to

chance, but that the determining environmental factors are highly contingent on the locality of the pond.

Introduction.

Ponds are important in landscapes throughout much of the world. Evidence from ponds in Europe suggests that they support disproportionately high numbers of invertebrate and plant species given their small size compared to larger freshwater habitats (Williams et al. 2004). This arises because individual ponds typically support varied communities; even ponds close together can contain markedly different communities of protists, plants and animals (Brian et al. 1987, Friday 1987, Jeffries 1998, Angelibert et al. 2004, Andrushchysyhn et al. 2003, Briers and Biggs 2005) so that the overall diversity within the pondscape (Boothby 1997) is increased. This heterogeneity occurs despite the apparent dispersability of many pond taxa, even down to the genetic differentiation between populations of the same zooplankton species in adjacent ponds. This heterogeneity may be due to chance and historical events or deterministic processes which create apparently idiosyncratic outcomes. For example De Meester et al. 2002 proposed the Monopolisation Hypothesis to explain this paradox, whereby founder effects combined with rapid adaptation to local conditions by a species colonising a new pond creates a community highly resistant to later colonists. However there is lack of examples tracking the development of pond communities from their foundation; this paper provides such an example, describing spatial and temporal patterns over a ten year period and testing the importance of spatial and temporal variation of hydrological variation for the development of macrophyte communities

Whilst individual ponds may contain fewer species than comparable samples from rivers, i.e. the individual ponds' α diversity is lower, a distinctive feature of sets of ponds is the

heterogeneity of their plant and animal communities , i.e. the β diversity of ponds is greater (Williams et al. 2004). Ponds are therefore a good example of the more general ecological phenomenon of patchiness. Pond wildlife shows examples of many general patterns and processes that affect the wildlife of patchily distributed habitats, e.g. species turnover (Briers and Warren 2000), the influence of patch quality (Jeffries 2005), complexities of dispersal (Allen 2007) and the influence of distances between patches (Briers and Biggs 2005). An additional factor is that the ponds themselves may come and go in response to both natural variations, e.g. wet or dry years determining whether temporary ponds fill up or remain dry, and changes due to anthropogenic land use creating or destroying ponds.

The heterogeneity of ponds at local (Jeffries 1989), regional (Jeffries 1998) or national (Declerck et al. 2006) scales has provided a challenge to general models of how pond communities establish and develop. Many extensive surveys of ponds, sometimes featuring over 100 ponds and recording a wealth of variables which may determine local biodiversity, have identified broad relationships between communities and environmental influences e.g. pH or altitude. However these results often reflect extreme ranges in these variables which create broad patterns (e.g. acidophilous versus alkaline pond communities) but are poor at describing or predicting the distinctive, local variation between ponds with apparently similar environmental characteristics. For example Briers and Biggs (2005) found that environmental variation had little effect on pond invertebrate communities found across 102 ponds in Oxfordshire, UK, unless the variation was considerable. For pond plants Edvardsen and Okland (2006a, 2006b) found that both

species richness and composition of plants from individual ponds were only weakly related to environmental variables whilst Joye et al. (2006) were able to produce robust models of pond plant species' individual abundance for only 10 of 45 species selected for modelling.

The heterogeneity of ponds and lack of simplistic associations between many pond species and environmental variables has long been credited to the importance of chance events (Key 1893, Godwin 1923, Talling 1951, Jeffries 1989, Wilson et al. 1992, Boileau and Taylor 1994, Kazmierczak et al. 1995, Edvardsen and Okland 2006a, 2006b). This is an intuitively attractive explanation given the scatter of ponds across the landscape. However, this explanation may simply reflect how little we know about individual species' needs and tolerances. The contradictions are well illustrated in the author's own work, having explained the heterogeneity of pond wildlife by chance (Jeffries, 1989) but also as species-specific responses to pond habitats (Jeffries, 2005) which might create apparently diverse assortments of species although each species is responding deterministically to pond environments. In addition pond wildlife may be affected by historical events, e.g. an unusually dry year, unrecorded at the time and undetectable in retrospect which may confound analyses (Edvardsen and Okland 2006a, 2006b), especially in studies using the tradition of extensive surveys of many ponds with data collection confined to one year. Edvardsen and Okland (2006b) specifically suggest that time series of data from ponds will show that plants appear and disappear along with variations in biomass; however we lack examples. This paper presents just such a time series, recorded over a decade.

So, the spatial and temporal heterogeneity of ponds remains a challenge, both to our understanding of the fundamental ecology of ponds and to the conservation of these important habitats. There is evidence of spatial effects from recent studies specifically addressing this phenomenon. Briers and Biggs (2005) found significant spatial autocorrelation amongst macroinvertebrate communities, the effects strongest at shorter distances of a few kilometres but detectable up to 13 km. Sanderson et al. (2005) modelled the incidence of ten species of invertebrates from 76 temporary ponds, comparing the effectiveness of models which included a spatial component in addition to environmental data, e.g. pond area, to models based solely on the environmental data. Models including the spatial component were better for seven of the ten species and the spatial effects were significant at a local scale, over distances of <200m. There is some evidence for plant communities too. Linton and Goulder (2003) showed that numbers of macrophytes in a pond could be effectively modelled using numbers of species in neighbouring water-bodies within 500m as predictors, although this may reflect localised variation in species richness affecting all waterbodies in an area, rather than any interplay between the patches of habitat.

This study describes the spatial patterns of macrophyte communities in a set of thirty adjacent, temporary ponds, from their establishment up until ten years later. This created the opportunity to test the development of spatial patterns at the very small, local scale, their relationship to hydrology and the influence of historic events. The spatial and temporal patterns of communities within ponds were compared to variations in length of

summer dry phase and winter inundation. Data were examined to distinguish if relationships between hydrology and plant communities were ultimately determined by spatial position of the ponds or appeared to be the result of each ponds' chance history.

Methods and materials.

Field site and pond creation.

Thirty ponds were dug in a seasonally flooded field at Hauxley Nature Reserve, Northumberland, UK, (British National Grid NU 285 025) in the autumn of 1994. Each pond was $1m^2$, 30 - 40 cm deep in the centre and the 30 ponds laid out in a roughly triangular array across the field's gradient of seasonal inundation, over an area of 30 x 30m (see Figure 1). The size and proximity of ponds was designed to match wetland ponds showing high β diversity in previous studies by the author (Jeffries 1989, 1994) but whose history and variation prior to the studies was unknown; the Hauxley ponds would allow the role of historic events to be monitored. In addition the arrangement of ponds was intended to cover the hydrological gradient in the field so that conditions would vary between ponds but they were very close together so that distance should not be a restriction for colonization. All the ponds were dug in an area of the field vegetated with a thin, patchy sward of *Leptodictyon riparium* Hedw (Warnst.), *Agrostis stolonifera* L., *Alopecurus geniculatus* L. and extensive bare substrate, adjacent to an area of *Eleocharis palustris* L. and *A. stolonifera* which, in wet years, approximates to UK National Vegetation Classification S19 *Eleocharis* swamp (Rodwell 1995). The whole area within which ponds were dug was known to flood regularly in winter. Following the wet summers of 1997-1998 the area of *E. palustris* and *A. stolonifera* expanded into a distinct, closed sward around ponds on the south side of the array (Figure 1) whilst ponds on the northern side remained in amongst a more terrestrial community.

Ponds filled with water within 24 hours of being dug. The ponds are within 10-50m of larger permanent and temporary ponds and the whole site is at the northern end of a 10 km complex of high quality wetland protected areas along Druridge Bay. Small, temporary ponds are commonplace throughout the coastal habitats of south-east Scotland and eastern England, usually as part of dune slacks or freshwater wetland complexes. These habitats are usually inundated by mid autumn, the small pools linked up under larger flashes of water, which then dry out in spring leaving isolated pools which dry completely in July or August in most years.

Sampling.

Macrophyte vegetation. Vegetation in the ponds was recorded in late May/early June, the dates varying depending on how quickly ponds were drying out. A $1m^2$ quadrat with grid-wires at 10 cm intervals was laid over each pond and used as a point quadrat, giving 81 point samples per pond, recording all the vegetation beneath each grid-wire intersection. Plants were recorded as species except for *A. stolonifera* and *A. geniculatus*, which could not be reliably separated when not associated with flower heads. These two grasses were treated as one taxon in subsequent analyses, although *A. stolonifera* was much more widespread and abundant on site. In addition occasional small terrestrial herbaceous seedlings too small to identify were recorded as "unidentified seedling". The point samples were rescaled to % cover for subsequent analyses.

The early summer vegetation recorded for this study was typical of the ponds throughout the year. Anecdotal records from the winters preceding each summer sample showed that

the ponds contained similar vegetation to the summer, but that the macrophytes were less extensively developed as plants were usually recovering from summer dry phases. The differences between the vegetation in winter and summer were of biomass, not of incidence or relative dominance.

Pond hydrology. The lengths of time that individual ponds dried out in summer or were joined together by winter inundation across the site were recorded as days. Ponds were visited throughout the year and each pond was recorded either as inundated (i.e. overflowing sufficiently to connect with some of the other ponds), wet (some standing water but separate from all other ponds) or dry (no standing water). Times of drying or flooding were measurable to within at least 3 days, sometimes more precisely. Figure 2 shows the extent of drying out or flood linkage of the 30 ponds per month from 1995 to 2004, measured as mean number of days that ponds were dry or linked by flooding per month. During the period of this study there was considerable variation in local hydrology. 1995 and 1996 were the end of a period in the UK often described as the early 1990s drought (Gibbins and Heslop 1998) whilst in 1997 Northumberland witnessed unusually heavy early summer rainfall, of perhaps a 1 in 1250 year return time preventing summer drying and resulting in sustained flood link between ponds throughout 1998 (Wheeler 1999).

Spatial position of ponds. The distances between ponds were measured from the centre of each pond to the centre of all the others.

Analyses.

Describing the plant communities. The macrophyte communities recorded from the thirty ponds between 1995 and 2004 were classified using TWINSPAN. All 300 records (30 ponds, ten years) were analysed together to identify variation between ponds but also how individual pond communities may change with time, switching between TWINSPAN end-groups. TWINSPAN was run testing different pseudospecies cut levels, all of which produced broadly the same initial two groups. Cut levels of 0, 2, 5, 10 and 20 were used for the analyses presented here; higher cut level thresholds resulted in a few large, ecologically incoherent groupings. The eight TWINSPAN end groups selected here were chosen because they consisted of recognisable communities and time periods with indicative dominant species. Differences between TWINSPAN groups were tested using ANOSIM (Clarke, 1993). TWINSPAN and ANOSIM were run on Community Analysis Package (CAP) 3.0.

Analysing spatial patterns. The spatial patterns of the plant communities within each year were analysed using the Mantel test. For each year the plant communities within the ponds were compared using the Bray Curtis index of dissimilarity. The Mantel test was then used to compare the correspondence of differences between ponds with spatial distance apart. The Mantel test was also used to test for spatial differences in the length of summer dry phase and winter inundations each year. Mantel tests were run on PC ORD 3.0.

Partial Mantel tests were used to investigate any correspondence between plant communities and the preceeding year's summer dry phase or winter inundation, by firstly factoring out possible spatial effects and then comparing directly comparing differences in plant communities with differences in length of dry phase (see Smouse et al. 1986, Fortin and Gurevitch 2001 for details of partial Mantel tests). For each year the Bray Curtis dissimilarity measures between ponds were regressed against distance between ponds and the standardised residuals saved. Similarly the differences in length of summer dry phase or winter inundation between ponds were regressed against distance between ponds and the standardised residuals saved. The relationship between plant communities and preceding dry phase or inundation was then explored by using the Mantel test to compare the matrices of Bray Curtis residuals versus the residuals of the previous summer's dry phase or winter's inundation.

Results.

Plant communities. Twenty two species of macrophytes were recorded from the ponds between 1995 and 2004 although only nine species were widespread or abundant; *Spirogyra* sp., *Chara vulgaris* L., *Leptodictyum riparium*, *Ranunculus aquatilis* L., *Juncus articulatus* L., *Glyceria fluitans* (L.) R. Br., *Agrostis stolonifera* and *Eleocharis palustris*. Six of the twenty two were occasional terrestrial herbs usually colonising dried ponds e.g. *Ranunculus repens* L. as small seedlings.

Individual species and communities showed distinct spatial and temporal variation over the ten years (see Figure 3 for examples of % cover, Figure 4 for species' incidence and

Figure 5 for distributions of TWINSPAN groups between the ponds in 1995, 1998, 2000 and 2004.).

In the first year most ponds contained only scattered strands of *L. riparium* sometimes with straggling *A. stolonifera* leaving most of the substrate bare, although many species were widespread across ponds (e.g. *Spirogyra* and *L. riparium*, Figure 4). By 1996 several species had established and *C. vulgaris*, *L. riparium*, *R. aquatilis* and *A. stolonifera* were widespread, although % cover remained patchy (Figures 3 and 4). From 1997 onwards more distinct communities became apparent in particular a difference between those ponds whose substrate was covered with a dense sward of *L. riparium* (often with either *G. fluitans* or *E. palustris* as a sub-dominant) versus those ponds retaining exposed substrate covered, in early summer, by clumps of *Chara vulgaris* or *Ranunculus aquatilis*. Ponds dominated by *L. riparium* moss were originally concentrated in the south-west side of the array of ponds in amongst the *A.stolonifera/E. palustris* sward but these moss dominated communities spread to other ponds over the ten years and were the most widespread by 2004 (Figure 5d). *Chara vulgaris* and *R. aquatilis* ponds were increasingly marginalised along the north east edge of the ponds. The incidence of *C. vulgaris* shows particular decline (Figure 4f) whilst *E. palustris* showed sustained spread (Figure 4e). This sequence is not a straight forward linear succession. Wet summers in 1997 and 1998 resulted in no dry phase in 1998 and ponds held water from May 1997 to June 1999. *Spirogyra* sp. became widespread and dominant, forming thick mats over the tops of many ponds and, at the same time, the incidence and % cover of *L. riparium* declined (Figure 3a *Spirogyra* sp. versus 3c *L. riparium.* Note also the

wide spread of *Spirogyra* sp. dominated TWINSPAN group 13 in Figure 5b). However the return of dry phases in the summer of 1999 ended *Spirogyra's* dominance.

TWINSPAN separated ponds into coherent groups after three rounds of division corresponding to the visible changes in the ponds over the years (Table 1). The first division separated those ponds dominated by moss swards from those dominated by *C. vulgaris* or *Spirogyra* sp. Subsequent divisions distinguished groups by time (e.g. Group 9 are ponds that were eventually dominated by moss but in the early years of the study before the thick swards developed) or by sub-dominant (e.g. groups 10 and 11 which are dominated by moss but with *G. fluitans* or *E. palustris* as sub-dominants respectively). ANOSIM results suggested that all eight end groups were significantly different to each other, with dissimilarities between groups of >80% in 22 out of 28 pair-wise comparisons (Table 2). Within groups similarities were lower, between 30-70%, Table 1) although most groups have one dominant species (Table 1 gives % cover for all species with mean cover >10% cover within a group).

Spatial patterns. Mantel tests suggested that the plant communities in individual ponds showed significant spatial patterns in eight of the ten years (Table 3). The Mantel r statistics were positive in every case, i.e. the Bray Curtis dissimilarity measures increased with increasing distance between ponds. This accords with the general patterns shown in Figure 5, as communities change across the array of ponds from the moss dominated ponds at the south-west of the array to the *C. vulgaris* and *Spirogyra* sp. ponds towards the north-east. This spatial pattern also changed with time as the moss dominated

communities established in more ponds (Figure 5b, c and d). This spatial distribution of plant communities followed the same pattern as the winter inundation, spreading from south-west to north-east.

The duration of winter inundation showed significant spatial variations in every year. Inundations joining ponds always started amongst the ponds at the south-west side of the array, spreading northeastwards and then retreating back southwards in spring (Figure 1). In contrast the length of the summer dry phase only showed significant spatial patterns in three of the nine testable years (and in the remaining year, 1998, no pond dried up). In all three years in which dry-phase showed significant spatial patterns the differences in duration of dry-phase increased with distance between ponds. Partial Mantel results testing the relationship between differences in winter inundation and differences in plant communities, having factored out spatial position, were not significant in any year, the r statistic was 0.0000 in every case (Table 3). Partial Mantel tests examining the correspondence between plant communities and the length of the preceding summer's dry phase were only significant in one year out of the eight which could be tested (Table 3). These results suggest that whilst the plant communities and the winter inundation both show coincident spatial patterns this is because each pond's hydrology is determined by spatial position of the pond within the field. The position of each ponds in the field is the important factor, ultimately determining local hydrology, even if the hydrological variation was then a proximate cause of macrophyte heterogeneity between ponds.

Discussion.

The thirty small ponds supported a variety of different macrophyte communities over the ten years of this study and these communities showed distinct spatial and temporal patterns.

Spatial and temporal patterns of the plant communities. The distribution of communities between ponds showed significant spatial patterns in most years, generally becoming less similar with increasing distance. These patterns were not fixed throughout the study period. In the first two years most ponds contained small fragments or seedlings of plants encroaching from the surrounding field (Figure 5a, group 9) but by 1998 the south-western ponds contained almost continuous *L. riparium* swards over their substrate (Figure 5b, groups 10 and 11) whilst the north-eastern ponds were dominated by *Spirogyra* sp. and *C. vulgaris* (Figure 2c, groups 13, 14 and 15). The communities within most ponds showed successional sequences as additional species established and also increased extent of dominant species. The spatial distribution of communities changed as communities dominated by *L. riparium* moss established in more ponds, excluding the *C. vulgaris* and *R. aquatilis* communities which were more widespread in the first three years (Figure 2c and 2d). However some ponds remained free of moss even after ten years. Changes throughout time were not only linear successional in character. During the unusually wet summers of 1997-1998 ponds were increasingly dominated by *Spirogyra* sp., which seemed to smother the development of most other species. All these spatial and temporal patterns occur in pondscape of only 30 x 30m; the results may provide some insight into the heterogeneity of ponds at the landscape scale. If such distinct heterogeneity can emerge at the intimate scale of the Hauxley ponds in one field, then the

greater environmental variation across wider landscapes is likely to promote the considerable β diversity of ponds at larger scales.

The value of a pond cluster for sustaining local β diversity. The spatial heterogeneity of plant communities between the ponds within any one year was probably greater than would be provided by one, larger pond dug out over the whole of the same area. This result supports data from regional surveys which have suggested that pond clusters may be better than single, larger ponds for promoting local species richness (Jeffries 1991, Oertli 2002). Two nearby larger ponds created in 1995-1996 in the same field as the study ponds started out as diverse mixes of emergent and submerged plants but by 2004 were both entirely dominated by the same *L. riparium* sward which came to dominate a majority of the smaller ponds. The communities of the *C. vulgaris* and *R. aquatilis* ponds were unlikely to survive as subhabitats within a single larger pond once *L. riparium* had establised. *Leptodictyon riparium* appears to be a dominant competitor, apparently smothering other submerged species, in the same way that *Sphagnum* mosses appear to be able to exclude vascular plants (Urban 2005). The Hauxley ponds without a moss sward dried out to leave exposed, hard-baked substrate whilst those covered with *L riparium* stayed damp underneath the moss and the substrate became conspicuously black and foetid compared to the ponds where substrate was left exposed. Once a thick moss sward was established plants such as *C. vulgaris* or *R. aquatilis*, which regrew annually after summer dry phase, appeared to be unable to survive in these conditions. Germination of *Chara* oospores and the subsequent establishment of germlings is known to require sufficient light (varying with species, e.g. de Winton et al. 2004, Kalin and

Smith 2007, Sederias and Calman2007) which may be restricted underneath the moss. In addition *Chara* species may also fail in fine, organic rich sediments, such as those which develop under the blanket of moss (Matheson et al. 2005).

Pond species richness generally shows only a weak, often insignificant relationship, with area, although this lack of a significant pattern appears to be more common place for invertebrates than plants (e.g Helliwell 1983, Jeffries 1991, Oertli et al. 2002, Hinden et al. 2005, Sondergaard et al. 2005. However see Rundle et al. 2002 and Sanderson et al. 2005 for examples of area as significant for invertebrate community composition). For many sites a cluster of small ponds will provide a valuable (high species richness) and practical (easy to dig due to small size) conservation strategy, whilst also recognising that some isolated and large ponds are still valuable in case their unique communities are ignored or replaced with dense clusters of small ponds (Scheffer et al. 2006).

Inter-annual variation and the role of historic events in the development of the ponds' communities. The spatial patterns changed over time, providing a rare recorded example of spatial dynamics over ten years, although at a very small scale. Some of the changes within ponds were familiar successional processes. For example *Chara* species are often described as pioneer species (e.g. Fleury and Perrin 2004) and *C. vulgaris* was widespread in the first few years, although incidence declines over the ten years. Alternatively *E. palustris* is a later successional species in these ponds and takes several years to become widespread, but was found in over twenty ponds from 1999 onwards (Figure 4e). The general trend of replacement of *C. vulgaris* or *R. aquatilis* communities by *L. riparium* was disrupted in 1998 and 1999 as thick mats of *Spirogyra* sp. were able

to grow throughout the summer of 1998 due to the lack of a dry phase. Some invertebrates did not colonise or went extinct from ponds clogged with *Spirogyra* sp. (Jeffries 2005), an example of short term events which may be difficult to interpret without knowing the history of a site (Edvardsen and Okland 2006a). The thick *Spirogyra* sp. mats did not re-appear after the re-establishment of dry phases in 1999 and the plants and invertebrates which had suffered during the dominance by *Spirogyra* sp. returned in subsequent years. These changes suggest that the wildlife of temporary ponds may be adversely affected by ponds becoming permanent, either through changes to local hydrology or intentional management practices such as deepening ponds.

The spatial patterns change over time, the inter-annual hydrological variation altering the competitive balance between species and the species themselves changing the environment within the ponds. The ten year time span of this study gives an insight into the temporal heterogeneity of pond types. Distinct communities developed very quickly and there remained a marked variety of plant communities after ten years. If the ponds had been surveyed as part of a snap-shot extensive survey the differences between many of the individual ponds would have been striking, as in published studies (e.g. Friday 1987, Jeffries 1991, Williams et al. 2004), and this heterogeneity might have been credited to stochastic processes, but snap-shot data from different years would have given very different outcomes.

Deterministic development of the local scale pond heterogeneity. The spatial pattern of macrophyte communities in the Hauxley ponds suggests some underlying deterministic

process, in particular the initial establishment of *L. riparium* dominated communities towards the southeast of the pondscape, and the subsequent changes as these moss-dominated communities spread across the site. However precise causes remain uncertain. When the ponds were dug they all appeared to lie within an area of scattered grasses and moss with extensive bare soil but with no visible differences in the substrate as ponds were dug out. Winter inundation shows significant spatial variation, always longer at the south-west of the array of ponds. The longer inundation of these south-western ponds, along with the annual spreading of floodwaters north-east over the ponds coincides with the spatial pattern of the ponds within which moss originally established and the subsequent spread of moss dominated communities into other ponds. After the wet years of 1997 and 1998 the south-western ponds were enclosed within a much more distinct area of *A. stolonifera*/*E. palustris* wetland and *L. riparium* was able to gain complete dominance in the ponds within this area. It is unlikely that the inundation linking ponds affected the spatial pattern of communities by simply allowing *L. riparium* to spread to new ponds because the moss was found in the majority of ponds from the first year onwards (Figure 4c). Nor does inundation alone show any relationship to plant communities once the strong spatial trend to the flooding is factored out (partial Mantel test, Table 2). Instead the spatial variation in inundation is created by the local geomorphology and spatial pattern of ponds at the site. The *A.stolonifera/E. palustris* sward which surrounded the south-western ponds from the beginning of the study, and the spread of inundations outwards from this core in most winters, may have created distinct physicochemical gradients, as the deeper water submerged ponds, saturated substrate and perhaps altered the local physicochemical environment allowing the moss

community to become dominant. The results suggest that the spatial variation of the plant communities arises from the precise location of each pond and how this determined an individual pond's hydrology. Small-scale differences between ponds create distinct communities. The macrophyte community outcomes are deterministic but contingent on where each pond is.

Seen over the ten year time span, the succession of metacommunities between ponds at Hauxley appears predictable, in particular the spread of moss dominated communities. The heterogeneity of pond communities in 2004 does not appear to be chance when the history of the previous nine years is known.

There is evidence of spatial influences on the distributions of pond plants and invertebrates operating at landscape scales of thousands down to below hundreds of metres (Linton and Goulder 2003, Briers and Biggs 2005, Sanderson et al. 2005). The results from Hauxley show spatial patterns in the distribution of macrophyte communities is determined by even smaller scale variations across a pondscape. The results are from just one site and over a very small spatial scale compared to most pond surveys. Given that environmental variation should be considerably greater over the wider landscape these local scale results suggest that ponds over a regional scale would harbour very different communities as each responds to variation in its local environment. The results also suggest that this variation may be more deterministic than we had assumed and that the spatial position of a pond and its immediate, intimate surroundings are important factors determining pond plant communities.

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Table 1. TWINSPAN groups for all ponds 1995-2004. The main group characteristics are outlined at each division. For the final eight groups (groups 8-15) additional data are mean within-group similarity (Mean sim. %) and the mean % cover for all taxa in a group with mean cover of >10%.

Group 2. Ponds dominated by *L. riparium*				Group 3. Ponds dominated in different years by *C. vulgaris* or *Spirogyra* sp.			
Group 4. Ponds in early years, 1995-1997, with initial patches of *L. riparium*		Group 5. Ponds in later years with largely complete *L. riparium* sward in later years		Group 6.		Group 7	
Group 8	Group 9	Group 10	Group 11	Group 12	Group 13	Group 14	Group 15
6 ponds, throughout the 10 years with *R. aquatilis*, lacking extensive *L. riparium*	49 ponds, nearly all of them from 1995 – 1997 with initial, incomplete *L. riparium* swards	61 ponds, from 1998-2004 dominated by moss sward with extensive *G. fluitans*.	55 ponds, from 1998-2004 dominated by moss sward with extensive *E. palustris*	20 ponds, largely 1996-1997, with limited cover of *R. aquatilis*. Lack *Spirogyra* or extensive *C. vulgaris*.	39 ponds, largely 1996-1998 with extensive *Spirogyra* and some grasses and *C.vulgaris*.	28 ponds, largely 1999-2000, with extensive *C.vulgaris* and some grasses, rushes and *Spirogyra*.	42 ponds, throughout the 10 years dominated by *Spirogyra* and very few other plants

Mean sim. = 32.7%	Mean sim. = 43.4%	Mean sim. = 70.0%	Mean sim. = 56.7%	Mean sim. = 31.1%	Mean sim. = 53.0%	Mean sim = 33.0%	Mean sim = 53.2%
R. aquatilis 17.0%	*L. riparium* 33.2% *Agrostis/ Alopecurus* 16.9%	*L. riparium* 90.9% *G. fluitans* 50.1% *E. palustris* 15.6%	*L. riparium* 73.3% *E. palustris* 30.6% *Agrostis/ Alopecurus* 22.1%	(No plants >10% mean cover)	*Spirogyra* 60.6% *Agrostis/ Alopecurus* 18.3% *C. vulgaris* 17.7%	*C. vulgaris* 43.7% *E. palustris* 15.3%	*Spirogyra* 69.1%

Table 2. Differences between TWINSPAN groups. Between-group differences are given as % dissimilarity (Dissim) for each pair-wise combination. Differences between groups were tested using ANOSIM and the results are shown as the ANOSIM R statistic for each pair-wise combination, with significant differences indicated by * P<0.05, ** P<0.01 and *** P <0.001.

Twinspan group number	8					
9	Dissim. 86.3% R = 0.670***	9				
10	Dissim. 93.4% R = 0.998***	Dissim. 69.8% R = 0.660***	10			
11	Dissim. 89.1% R = 0.880***	Dissim. 68.9% R = 0.447***	Dissim. 48.2% R = 0.328***	11		
12	Dissim. 80.0% R = 0.446***	Dissim. 78.0% R = 0.474***	Dissim. 90.1% R = 0.927***	Dissim. 86.8% R = 0.836***	12	
13	Dissim. 91.6%	Dissim. 86.1%	Dissim. 86.7%	Dissim. 83.1%	Dissim. 82.6%	13

	R = 0.958***	R = 0.753***	R = 0.948***	R = 0.807***	R = 0.783***		
14	Dissim. 88.9%	Dissim. 92.3%	Dissim. 90.5%	Dissim. 83.3%	Dissim. 83.9%	Dissim. 75.4%	14
	R = 0.561***	R = 0.776***	R = 0.925***	R = 0.718***	R = 0.441***	R = 0.496***	
15	Dissim. 92.7%	Dissim. 97.0%	Dissim. 94.0%	Dissim. 91.0%	Dissim. 90.7%	Dissim. 53.0%	Dissim. 80.4%
	R = 0.774***	R = 0.891***	R = 0.930***	R = 0.843***	R = 0.734***	R = 0.147***	R = 0.518***

Table 3. Results of Mantel and partial Mantel tests for each year. The subject of the test is described in the left hand column. Results are given as the r statistic; ns, not significant, * P<0.05, ** P<0.01 and *** P <0.001.

	Year									
	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Subject of Mantel test										
Plant communities' Bray Curtis dissimilarity indices	r = 0.132 *	r = 0.161 **	r = 0.167 **	r = 0.345 ***	r = 0.477 ***	r = 0.140 *	r = 0.105 *	r = 0.072 ns	r = 0.089 ns	r = 0.203 **
Length of winter inundation links	r = 0.564 ***	r = 0.535 ***	r = 0.508 ***	r = 0.396 ***	r = 0.332 ***	r = 0.541 ***	r = 0.556 ***	r = 0.285 **	r = 0.301 ***	r = 0.171 *
Length of summer dry phase	r = 0.353 ***	r = 0.022 ns	r = 0.094 ns	(No summer dry phase in 1998)	r = 0.054 ns	r = 0.091 ns	r = -0.002 ns	r = 0.194 **	r = 0.102 *	r = 0.0164 ns
Partial Mantel test										

Plant Bray Curtis indices vs length of preceding winter inundation	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns	r = 0.000 ns
Plant Bray Curtis indices vs length of preceding summer dry phase	(No test, ponds did not exist in summer 1994)	r = 0.061 ns	r = 0.041 ns	r = 0.174 ns	(No 1998) summer dry phase)	r = -0.049 ns	r = -0.070 ns	r = -0.005 ns	r = -0.076 ns	r = 0.226 *

Figure titles.

Figure 1. The Hauxley pondscape; spatial array of the 30 ponds. ■ = position of individual pond ■ Initial extent of *Agrostis stolonifera/Eleocharis palustris* sward, ■ extent of *A. stolonifera/E. palustris* sward after wet years 1997 and 1998. The ═► arrow shows direction from which winter inundation spreads out northeastward over the array of ponds from start point amongst south-western ponds.

Figure 2. Hydroperiods for all 30 ponds summarised per month throughout the study, 1995 to 2004. During this period ponds were recorded in one of three conditions (1) inundated, joined to other ponds, (2) holding open water but not overflowing, or (3) dry. Data are plotted as mean number of days per month that ponds were either flooded (+ve departures from the horizontal zero line) or dry (-ve departures from zero line). When all ponds held water throughout a month but without linking up then the data are plotted at zero.

Figure 3. % cover of (a) *Spirogyra* sp., (b) *Chara vulgaris*, (c) *Leptodictyum riparium*, (d) *Ranunculus aquatilis*, (e) *Eleocharis palustris* and (f) *Glyceria fluitans* in the thirty ponds 1995-2004, mean % cover ± one standard error.

Figure 4. Incidence of (a) *Spirogyra* sp., (b) *Chara vulgaris*, (c) *Leptodictyum riparium*, (d) *Ranunculus aquatilis*, (e) *Eleocharis palustris* and (f) *Glyceria fluitans* in the thirty ponds, 1995-2004.

Figure 5. Distribution of macrophyte communities throughout the thirty ponds in (a) 1995, (b) 1998, (c) 2001 and (d) 2004. The position of each pond in the field is shown by one of the symbols, but the precise symbol changes to represent the changing plant communities found in a pond in that year. Different symbols represent the different plant community groups defined by TWINSPAN (see Table 1 for summary of groups). Group symbols; ponds dominated by ● group8, ○ group 9, Δ group 10, ▲group 11, □ group 12, ■ group 13, ◊ group 14, ♦ group 15.

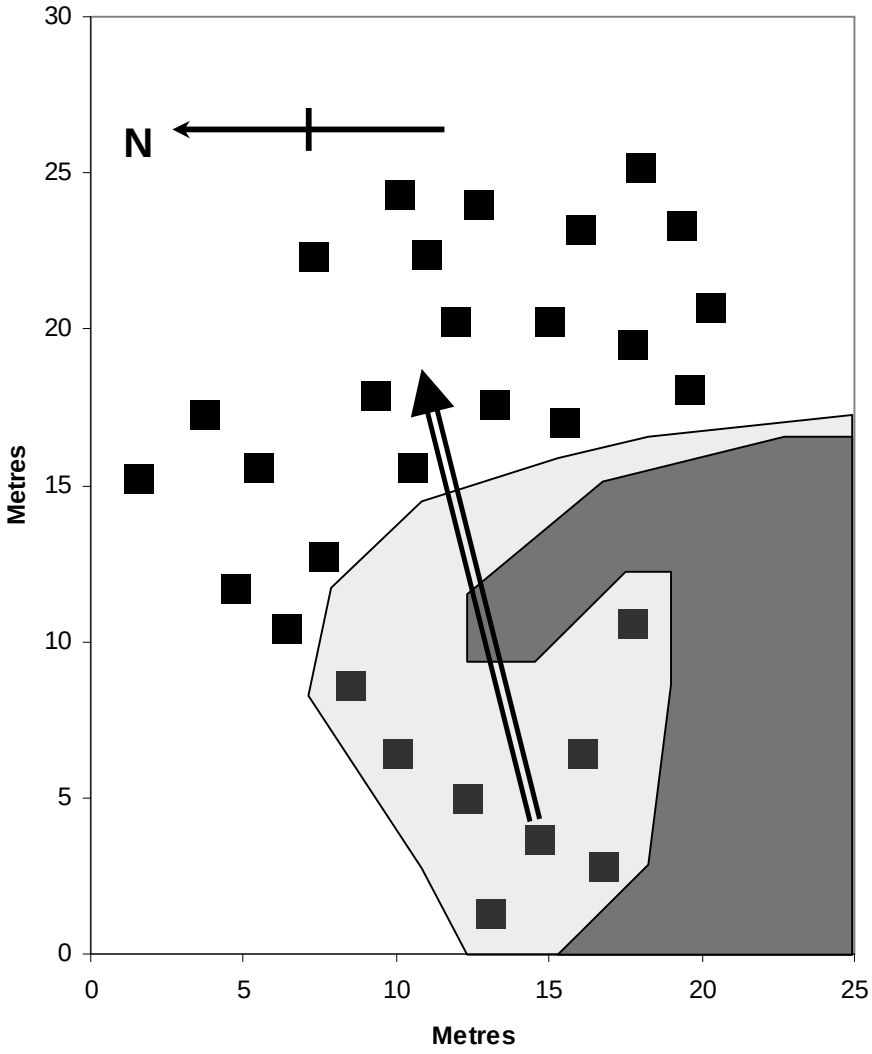


Figure 1

Figure 2

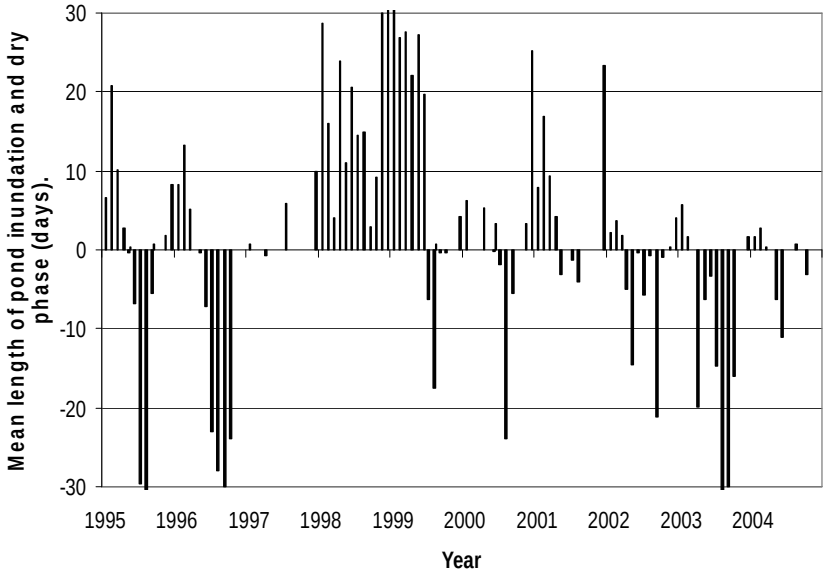

Mean length of pond inundation and dry phase (days).
30
20
10
0
-10
-20
-30
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
Year

Figure 3.

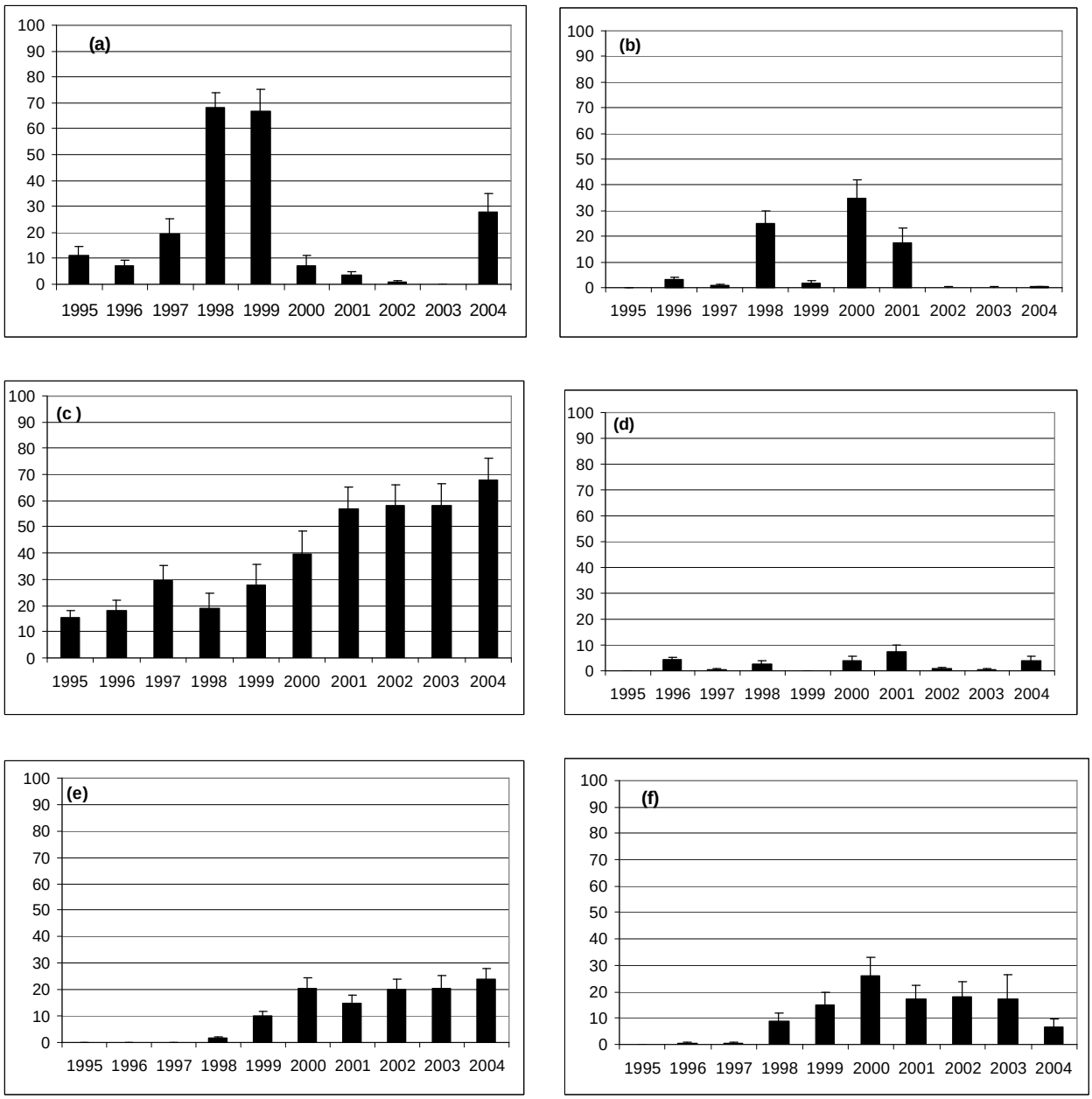

(a)
(b)
(c)
(d)
(e)
(f)
100
90
80
70
60
50
40
30
20
10
0
1995 1996 1997 1998 1999 2000 2001 2002 2003 2004

Figure 4

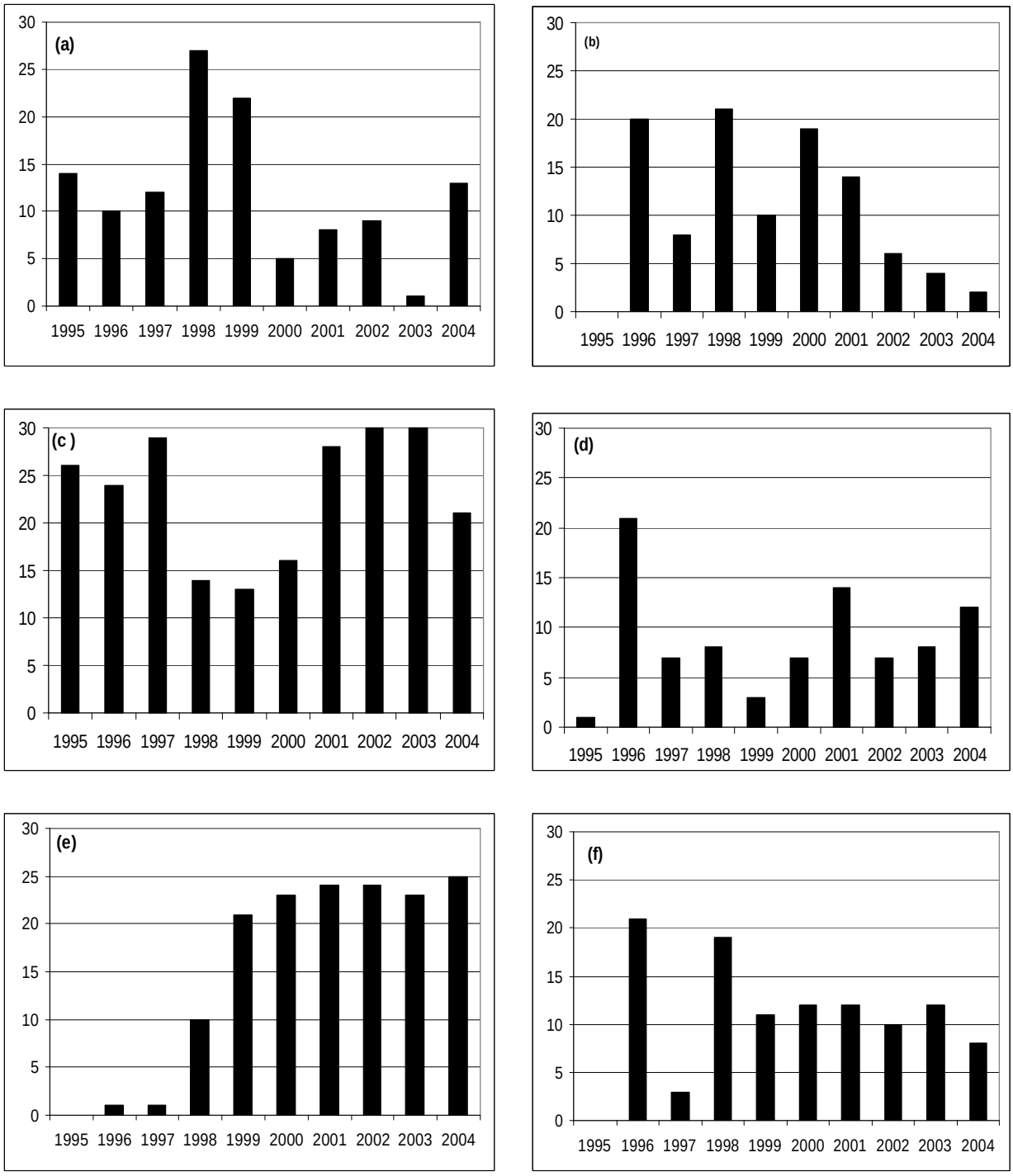
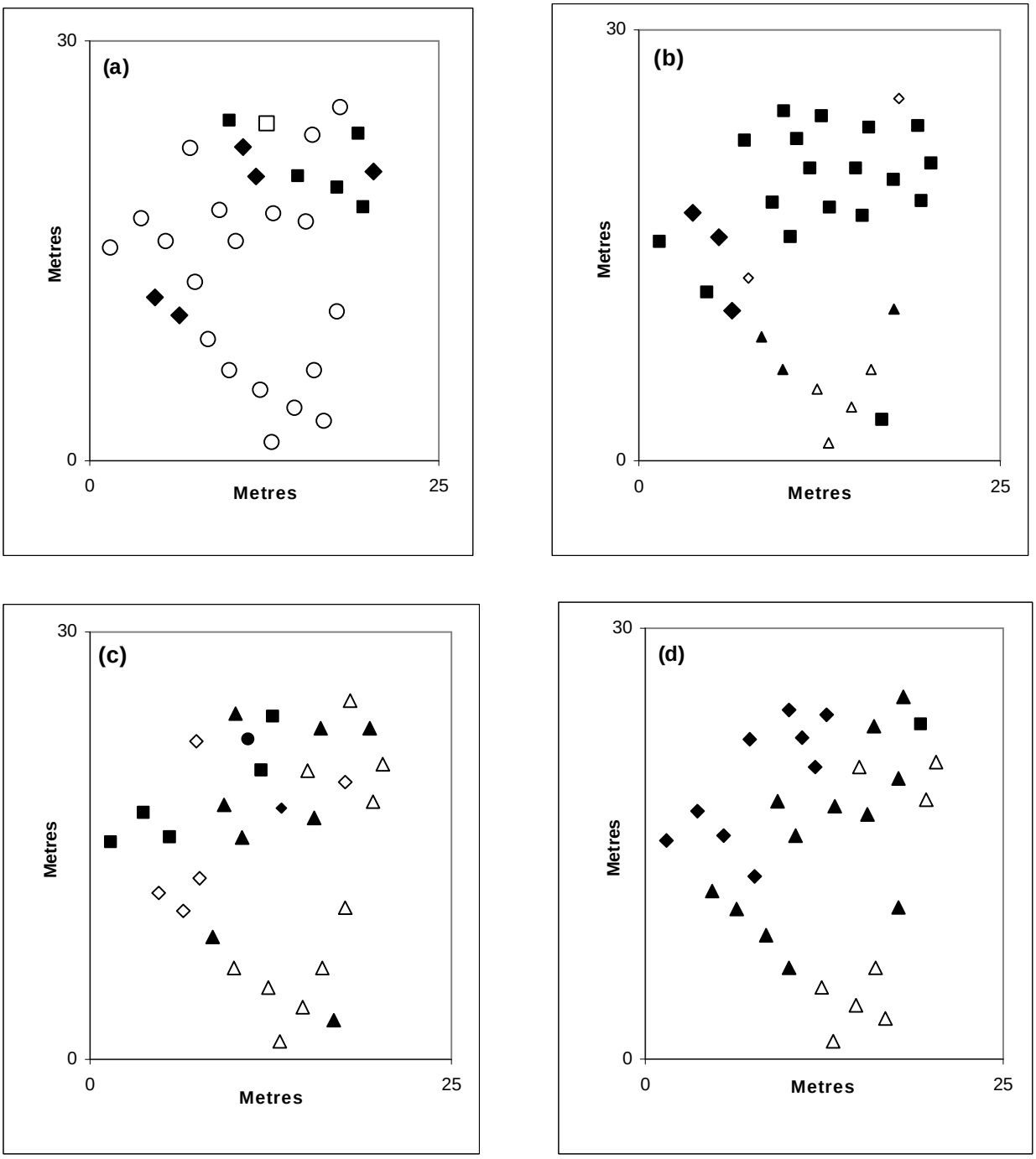

(a)
(b)
(c)
(d)
(e)
(f)
0
5
10
15
20
25
30
1995 1996 1997 1998 1999 2000 2001 2002 2003 2004

Figure 5


(a)
30
0
Metres
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25
Metres
(b)
30
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30
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